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ORTHOGENETIC SERIES INVOLVING A DIVERSITY OF MORPHOLOGICAL SYSTEMS.*

STUDIES IN DETERMINATE EVOLUTION. II.

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In the first paper† of the present series dealing with the evolution of plants, a general survey was given of the fundamental, progressive movements which have taken place in the entire kingdom. The present study deals with several examples of morphological structures which require the evolution of a complex reaction system to bring about the harmonious development of all the parts. These special cases have been selected not because they are exceptional but because they represent rather bizarre examples, illustrating a condition which confronts us on every side—a progressive movement resulting in the development of a more and more perfect system until the ultimate limit is attained, which in some cases gives a condition of over-adaptation, in others a structure very useful, apparently, to the individual, in others a very “useful device” which is however of no utility whatever to the individual in the matter of survival, and in still others a structure which has no special use at all. Each of the three examples given begins in a very slight movement and ends in a remarkably perfected consummation, which was of no importance in the first place and which could give no hint as to the remarkable end to which future steps would lead. As stated, such cases are present in great abundance all through the plant kingdom.

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†Schaffner, John H. The General Course of Evolution in the Plant Kingdom.

THE EVOLUTION OF A HIGHLY DEVELOPED BUR IN THE
PANIC-GRASS TRIBE.

(See Plate I.).

Grasses in general do not have any special bristles developed at the base of the spikelet. The structures are usually naked or merely pubescent with epidermal hairs. In the genus *Chaetochloa* and related groups a new structure appears which in its simplest expression is represented by the presence of one or two stiff cortical outgrowths or bristles at the base of the pair of spikelets. *Chaetochloa verticillata* (L.) Scribn. is a typical example (Fig. 1). In this species the bristles are retrorsely barbed, as frequently occurs in structures of this type whether they represent modified spines, prickles, sepals, petals, or other organs. Formerly the possession of such a peculiar structure, especially if some apparent use could be found for it, was a plain case of use or disuse or natural selection. In the case in hand, however, the grains enclosed in the flowering glumes fall away when ripe and the bristles with their retrorse hooks remain behind on the dying plant. Had the bristles been attached to the abscissed fruit, it would have been a plain case of utilitarian teleology to the credulous scientists of a generation ago. The important addition to the hereditary potentialities is something that is influencing the cortex to develop outgrowths when the ontogenetic gradient has reached the base of the pair of spikelets. The subsequent examples in this series will show how this peculiar character is increased step by step through a number of genera and many species.

Figure 2 represents *Chaetochloa imberbis* (Poir.) Scribn. which has 10 bristles at the base of the spikelets. These bristles are upwardly barbed, just the opposite from those of *C. verticillata*, and also remain behind on the old dead inflorescence when the spikelets are shed. If they were persistent on the abscissed spikelets, probably some one, still deluded by Lamarckian or Darwinian teleology, would claim that they were turned thus in order to prevent the bristles from clinging to passing beasts and men because they might thus be carried away too far and perhaps to an unfavorable habitat; since it is plain that they are in a favorable habitat already, otherwise the parent plant would not have survived to produce a crop of seed. Other species have bristles ranging between 2 and 10 and some have more.

In *Pennisetum glaucum* R. Br. there is not only an involucre of numerous stiff bristles and hairs around the base of the pair of spikelets (Fig. 3) but the cortical part of the stem bearing them is somewhat expanded. This represents a decided step in advance over the condition represented by *Chaetochloa imberbis*.

Figure 4 represents a low type of sandbur-grass, *Cenchrus myosuroides* H. B. K., which has a moderate development of prickles and a much more prominent cortical expansion round the spikelets. In figure 5, which represents the bur of our common sandbur-grass, *Cenchrus pauciflorus* Benth., the development of the basal cortical expansion is shown to have advanced decidedly and the prickles have become strong and rigid. The spines are retrorsely barbed and aid decidedly in helping the bur to hold on to one's toes or fingers and thus in being carried away from the favorable habitat of the parent plant to some possible, sterile ground where a cruel death may await the little sprouting embryos asleep within. Now, this bur is a very perfect device.

But there is still room for improvement, and the ideal is reached in such species as *Cenchrus palmeri* Vas. (Fig. 6) which has a very large prominently developed bur with large, long, stout prickles enclosing the spikelets with their ripe grain. Thus all these species and many others show a consistent orthogenetic movement from the very slight disturbance in the basal cortical development of *Chaetochloa verticillata* to *Cenchrus palmeri*. So far as the ability to get along in the world and to perpetuate itself are concerned, the last species is no better off than the first even though we have evolved a very ingenious structure to hold the seed as it comes from the parent plant. The first three important steps have no such use. So unless they were working for the good of the more highly perfected species of *Cenchrus* still to be evolved, it would be absurd to say that their first necessary steps were of any utility to themselves whatever. And there is also no evidence whatever that the elaborate bur is of any advantage to its possessor so far as a life and death struggle is concerned. For sandbur-grasses and foxtail-grasses grow side by side in the same field and the foxtails seem to be succeeding as well if not better than their neighbors with the perfect seed-holding device.

AN ORTHOGENETIC SERIES LEADING TO AN "ALABASTER BOX."
(See Plate II).

The Andropogoneæ, or beard-grasses, are even more extremely evolved than the panic-grasses just considered. It is, therefore, not surprising to find very remarkable peculiarities among them. The series which is outlined below represents the development of a box to hold the pair of spikelets and finally the mature grain. It is, in a broad sense, a device similar to the preceding case. But the box is produced by entirely different elements on a fundamentally different plan.

Many of the lower Andropogoneæ have quite ordinary panicles. The spikelets are in pairs, one stalked and one sessile. The specialization of these pairs of spikelets and their flowers presents a very interesting case of orthogenetic movement in itself in the various species series which will, however, not be considered here. In some of the less specialized genera, there is no special development of joints or abscission layers in the rachis below the pair of spikelets.

Passing from such species with continuous inflorescence branches, like *Miscanthus sinensis* Anderss., we come to forms represented by *Andropogon furcatus* Muhl. (Fig. 1) in which the branches of the inflorescence are very definitely jointed, and at maturity they are cut up into definite pieces by the formation of an abscission layer just below the insertion of the pair of sessile, grain bearing, and stalked, staminate spikelets. The rachis joint is slightly flattened on the side on which the spikelets are situated. Thus the first steps have been taken in the production of a typical crate for the grain in some future time and which may develop in some fortunate individuals which have advanced farther up the evolutionary ladder. The most important potentiality present is the ability to cut the material into suitable pieces at the proper places.

Figure 2 represents the rachis joint and spikelets of *Hemarthria fasciculata* (Law.) Kunth. The structure begins to have the first crude characteristics of a box. The rachis joint is flattened and somewhat excavated. The pedicel of the stalked spikelet is involved in this reaction and is usually grown to the edge of the rachis joint. The outer empty glume forms a respectable loose-fitting lid which is, however, too long for the box. The stalked spikelet is still entirely outside of the structure. In addition, another crude reaction which represents

a first step is evident in the articulation since the joints in Hemarthria are only tardily disarticulating. It is very commonly the case that both in important phylogenetic progressions as well as in trivial characters, the first steps are often imperfect, indefinite, or undependable. Just a little disturbance of the physiological states may cause either complete failure of the new hereditary expression or an imperfect expression. To find the promptness and decidedness of the abscission reaction, in contrast, one has only to go to the end of the series and examine a carpellate inflorescence of teosinte (*Euchlaena*).

Figure 3 represents a typical species of *Coelorachis*, *C. cylindrica* (Mx.) Nash. Here we have a box looking like the work of an amateur. The rachis is enlarged and deeply channeled; the abscission is definite; the stalked spikelet is greatly reduced and its flattened pedicel assists the lid in enclosing the fertile spikelet. The outer empty glume of the fertile spikelet is thickened and ornamented to some extent and forms an ill-fitting lid. The parts of the box fit better than the figure would indicate, since the "lid" and other glumes have been separated, for drawing, to show their nature more clearly. Other species of *Coelorachis* show the evolution of the box a little more perfected.

The gama-grass presents us with a well-evolved structure as shown in Fig. 4, *Tripsacum dactyloides* L. The rachis joints are enlarged and channeled out into deep troughs; the abscission is prompt and definite and the outer empty glume forms a well-fitting lid to close the opening; the carpellate spikelet with the mature grain is neatly boxed up. Were this structure about 10 times as long as it actually is, we could write an address on the side and, with the proper postage stamp, have it delivered through the mails to some distant office, confident in the fact that the parcel had been properly packed. Now the boxing up ability or potentiality has been properly attained by the adjustment and coordination of a large number of organs all of which had to evolve in the proper direction if the end result was to be attained. The box could be improved and beautified in various ways, however, and here we will find a principle at work that is of wide application in the entire realm of plant evolution. Evolution is above all perfective, and so cases are abundant where certain species have passed to this perfected ideal, often far beyond the limits of any real or imaginary

utility. There is no use of mincing words. These examples given are only selected cases out of great numbers of similar developments that any one can discover for himself if he is willing to spend 25 years of correct and intensive study in the taxonomy of plants.

The perfected box is attained in *Euchlaena mexicana* Schrad., or the teosinte, which stands at the limit of the Tripsacanae subtribe in many other respects. Figure 5 is a drawing of the mature boxed-up carpellate spikelet of this grass. This is a true "alabaster box." Both the modified stem and the modified outer empty glume, which represent the box and its lid, are highly indurated into a hard, crustaceous polished substance and there are also ornamental blotches or mottelings in evidence while in *Tripsacum* no such ornamentation is in evidence. The whole box has been rounded off so that the crude rough edges, so prominent in *Tripsacum*, have been removed; the abscission surfaces, not visible in the drawing, have been contracted into comparatively small areas; the lid fits perfectly, and, *mirabile dictu*, is clamped down by the inrolling of the edges of the box. The point of perfection of workmanship has been attained. The spikelet with its grain is perfectly encased. Determinate evolution has about reached its limit. There is one further possibility. The surface, instead of being smooth, might be ornamented as often occurs in highly evolved, indurated structures. This actually did take place in some related genera which however, did not get quite as far in general as teosinte. As stated, ornamental markings are abundantly to be found in indurated seeds, fruits and other hard structures. In the higher plants, ornamentation is commonly an accompaniment of the evolutionary movement of induration. Now compare Fig. 1. with Fig. 5. and you have a picture of the real process of evolution. All the related species of the series can be arranged in an orthogenetic order, the various species having positions at various levels of advancement.

Teosinte grows side by side with *Andropogons* which have no alabaster boxes for their grains. So far as survival is concerned, one is as well off as the other. The box is of no use to its possessor in a life and death struggle for existence any more than a gold watch keeping very accurate time is of importance for the survival of a savage. Nevertheless it is an ingenious, pretty box useful for holding the grain. In dis-

covering the facts of orthogenetic series we are not concerned about the relation of one step to another, nor about the order of the appearance of the steps. These are propositions that can never have any direct proof except such as may be gleaned from the imperfect paleontological record. Our chief concern is in the validity of the series in closely related groups of species and when we have discovered this we know that although we may have difficulty in tracing the origin of these processes to their ultimate internal causes, we can rest on the convincing reality of the phenomena without being led into a belief of childish superficial hypotheses as postulated in Lamarakism, in Darwinism, and in some of the more recently developed beliefs and fancies that would make of evolution a fortuitous process.

AN ORTHOGENETIC SERIES REPRESENTING THE EVOLUTION OF A
POLLEN BRUSH.

(See Plate III. All the figures magnified on the same scale).

The relation of insects to pollination is quite generally known even among the non-scientific. In the dark ages of the last century, scientists and others firmly believed that the special adaptations to insects were evolved by natural selection through the survival of the fittest. The plant was under the necessity of being pollinated if a following generation was to inhabit the earth and it was assumed that there was some profound advantage in cross-pollination while selfing was supposed to be injurious enough to cause elimination in the long run. The implications seemed perfectly evident to the credulity of the supposedly critical biologists of the period. Now when we find that large numbers of species both in the wind pollinated and insect pollinated series, and especially many with elaborate mechanisms which seem especially devised to lure insects, are either cleistogamous or completely parthenogenetic, the whole hypothesis of the evolution of such structures being caused by the necessity of cross-pollination passes over into the realm of fairy tales. The lower undifferentiated species of flowers nearly always succeed in being pollinated while many which have extreme adaptations do so with difficulty. If one takes an inventory of an undifferentiated flower type like a crowfoot or an anemony he finds that ordinarily it is difficult to find a flower that is not pollinated, while some

extremely specialized flower like the common milkweed has about one chance in eighty. The higher forms usually develop zygomorphy and this with other movements reduces the supply of stamens and pollen per flower. But the same movement of reduction occurs in wind-pollinated series. The orthogenetic series here considered cannot be questioned. But when we ask for causal relations we find that at every step in the evolutionary process one type of individual is just as successful as the other. They all have survival value. The one without even a hint of the adaptation gets along just as well as the one which has developed it, to the extreme degree. The relation between the actual evolutionary process in the plant and the insects is no more evident than the relation of the flea to the dog on which it lives happily. Yet just as the flea could not exist without the dog environment so none of these plants of the given series could exist without the insects. The series presented is taken from the mint family. Essentially similar series, differing in details of structural development but not at all in the efficiency of the devices appear in many orders and families of flowering plants.

Figure 1 represents an ordinary type of stamen with no special peculiarities. It is a stamen of *Agastache scrophulariaefolia* (Willd.) Ktz. All the remaining 11 figures of plate III. show steps in the evolution of the structure under consideration. Since the drawings are all on the same scale, the evolution of both size and structure will be apparent as a progression toward perfection.

Figure 2 represents a stamen of *Teucrium occidentale* Gr. In this stamen something is at work which separates the two parts of the anther. Now, of course, no one in his rational senses would see in this minute device any advantage over the preceding in securing pollination, especially no survival value in a life and death struggle. But here we do have a new phylogenetic potentiality introduced with a very slight reaction. We could not predict whither it would lead unless we actually saw the series evolved through the operation of its orthogenetic property.

In figure 3, *Clinopodium vulgare* L., a considerable advance is shown in the enlargement of the connective between the two anther-sacs and in *Satureia hortensis* L. (Fig. 4) the anther-sacs are still farther apart. In *Monarda didyma* L. (Fig. 5) the connective has enlarged decidedly and in such a way that the

anther-sacs are completely divaricate. In the meantime it is evolving to a decidedly zygomorphic condition so that there are only two fertile stamens left. A further advance in the zygomorphic nature of the flower bud will involve the one anther-sac of each stamen. The peculiar potentiality which is separating the two anther-sacs to a greater or less extent in various genera and species in this region of the mint family has no direct relation to the development of zygomorphy itself but is an independent mutative manifestation. To claim that these slight changes in the contiguity of the anther-sacs and the enlargement of the connective had produced an advantage of any sort to the possessor would be the height of absurdity requiring the same kind of credulity as is necessary for a belief in fairy tales.

Now, if our orthogenetic perfecting principle is correct as shown in the evolution of the grain box in the *Andropogoneæ*, we may expect some interesting developments in case the evolutionary movement continues to its determinate limit; and since the rapid progression of zygomorphy of the flower is in evidence, this property will also be involved in the further enlargement and elongation of the connective. The genus *Salvia* represents about the extreme in the evolutionary progression of the flower in the *Lamiaceæ*, and fortunately there are about 500 species, so there is abundant opportunity for the orthogenetic series to reach the limit. *Salvia lyrata* L. (Fig. 6), although it has the connective enormously elongated, when compared with *Monarda didyma*, is nevertheless about the lowest of our native sages. From this species on the various *Salvias* fall into gradation series in respect to the lengthening of the anther connective until a very extreme development is reached. In *Salvia lyrata* the one arm of the connective with its anther-sac is much longer than the other. The anther-sac of the short arm is still functional but much reduced. This is due to the influence of the zygomorphic nature of the flower as a whole. The flower bud is evolving determinateness more rapidly on the one side than on the other. In this example we have the first prominent steps, which if continued will evolve a perfect lever-brush apparatus. That there is any advantage to the flower in the elongated connective and its one sided development with a consequent reduction in the amount of pollen available for pollination is not at all apparent. In fact if there is any effect which might influence survival, it

would have to be regarded as a decided disadvantage when compared with the first species given, belonging to *Agastache*, *Teucrium*, *Clinopodium*, and *Satureia*, all of which have 4 functional stamens although the flowers are all zygomorphic to a greater or less extent.

Figure 7 represents a stamen of the common sage, *Salvia officinalis* L. The movements which produced the stamen of *Salvia lyrata* are carried on further, so the connective is much longer and the reduced anther-sac is very small, approaching the vestigial condition. In *Salvia lanceifolia* Poir. (Fig. 8) the vestigial anther-sac has entirely disappeared and the entire connective is now in the form of a lever but still imperfectly developed. Figure 9 represents a stamen of *Salvia farinacea* Benth. In this form, any one can see a decided improvement over the last species; and *Salvia pitcheri* Torr. (Fig. 10) is a still further advance toward the ideal structure. In Pitcher's sage the brush and lever works very perfectly. In fact, so far as the ability of the mechanism to brush pollen on the insect's back is concerned, nothing more can be desired. But the orthogenetic, evolutionary movement can go farther still in the same direction, provided a lengthening factor appears to give the proper length of corolla tube. There is in the stamen mechanism itself nothing to place a definite limit to further advancement. So in *Salvia splendens* Ker-Gawl (Fig. 11) we find a much more extreme development of the mechanism, which was possible because of the introduction of a lengthening factor operative in the corolla and style. One would think that at this point the brush and lever mechanism had certainly attained the limit. But there is a further step possible. Not only can the length of the connective be augmented decidedly so long as the corolla and style continue to enlarge and elongate in their evolutionary course but with the advancement of the zygomorphic nature, there can be developed a decided difference between the brush arm and the handle arm of the lever. This is a simple principle of elementary mechanics. Now since the handle end of the lever necessarily projects down into the corolla tube, there is little room for movement even when it is pushed to the extreme limit. But if the arm of the lever which holds the anther-sac is decidedly lengthened then a small amount of movement at the handle will give a wide arc of movement in the brush end, which no doubt would facilitate the throwing out or sprinkling of the pollen on the back of the

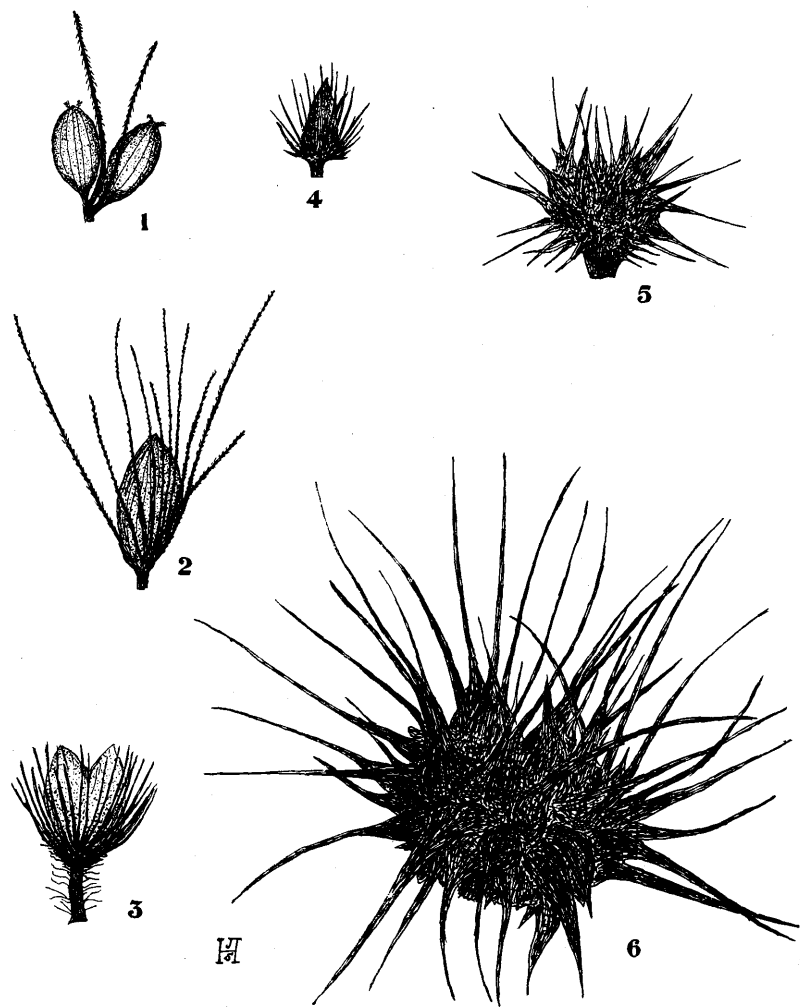
visiting insect. This remarkable perfection is attained in *Salvia patens* Cav. (Fig. 12.).

Compare Fig. 6 with Fig. 12 and we are again passing from a crude beginning to the ultimate of perfection. Evolution is perfective. Yet there is no ecological advantage in all this. So far as a mechanism to insure pollination is concerned, *Agastache scrophulariaefolia* works just as perfectly as *Salvia lyrata* and this works just as well as *Salvia patens*. The matter of survival is not involved at all. Any one looking for such a condition is simply exercising his credulity in opposition to the biological facts and results. The insects involved were part of the environment while the evolution was taking place. Their presence made such an evolution possible but the ecological interaction was not the cause of the appearance of the special potentialities developed. We see that all the different steps in the process have survived because not a single change involved the problem of survival, and because evolution proceeds through individuals. Had the proper insects been completely eliminated from the environment there would have been no advance because of the ensuing struggle for perpetuation. The old alone would have remained; for the old continues as before. It is very important to grasp the significance of this fact. For none of the imaginary causal factors of evolution, reaction to environment, natural selection, use and disuse, or geographic barriers is in evidence. The only way in which environment enters into the problem is the fact that the environment holds efficient insect pollen carriers. Since the environment was thus present, the orthogenetic progression could proceed to the extreme limit of the extreme *Salvias* without encountering the factor of elimination. Without the proper environment the very first step, which made pollination dependent on the presence of certain kinds of insects, would have led to destruction just as surely as the development of sterility in any individual line, whether plant, animal or human, necessarily brings an end of that particular line for all future time.

The three studies presented, which could easily be multiplied by the scores and hundreds, then plainly indicate that: Evolution is orthogenetic, perfective, and determinative.

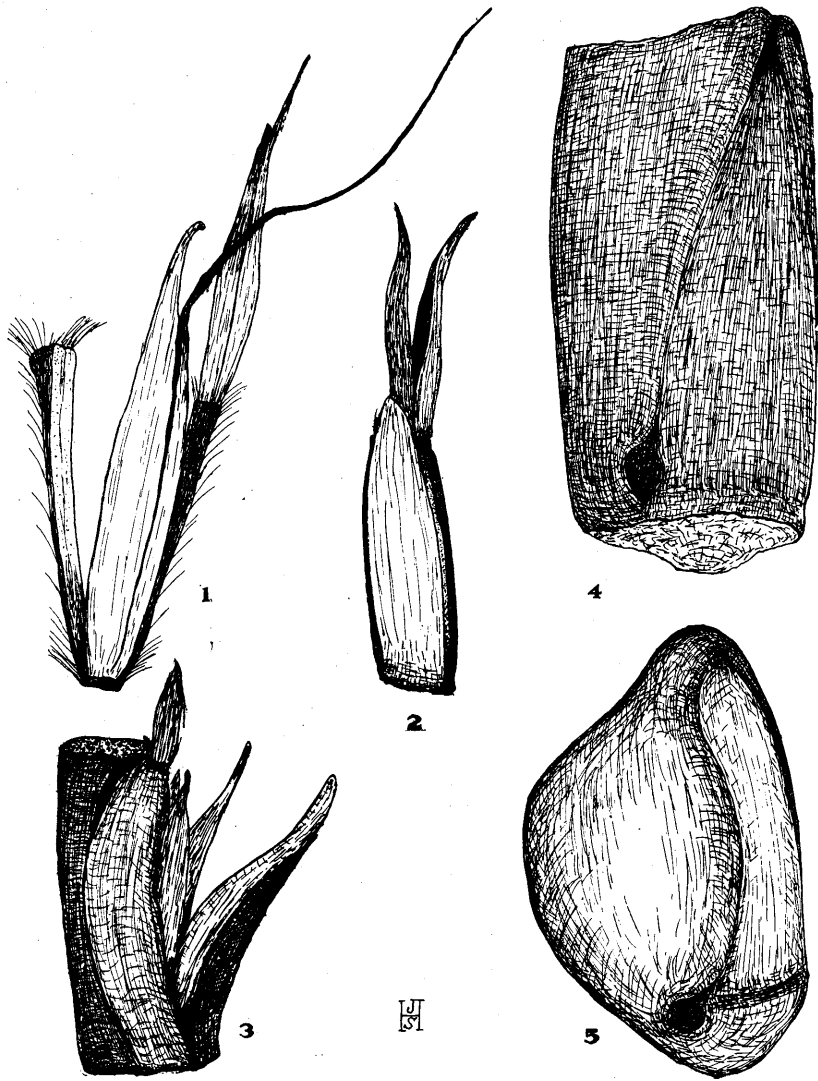
EXPLANATION OF THE FIGURES OF PLATE I.

- Fig. 1. *Chaetochloa verticillata* (L.) Scribn., showing two retrorsely barbed bristles at the base of the pair of spikelets.
- Fig. 2. *Chaetochloa imberbis* (Poir.) Scribn., with 10 bristles upwardly barbed.
- Fig. 3. *Pennisetum glaucum* R. Br., with an involucre of stiff bristles and hairs around the expanded base of the pair of spikelets.
- Fig. 4. *Cenchrus myosuroides* H. B. K., with a moderate development of the cortical expansion bearing a crown of prickles around the spikelets.
- Fig. 5. *Cenchrus pauciflorus* Benth., with a very pronounced cortical expansion and prominent prickles enclosing the two spikelets.
- Fig. 6. *Cenchrus palmeri* Vas., with a very large development of the cortical expansion bearing large long prickles, the spikelets being entirely enclosed in this highly evolved bur.



EXPLANATION OF THE FIGURES OF PLATE II.

- Fig. 1. *Andropogon furcatus* Muhl. A rachis joint with sessile and stalked spikelets.
- Fig. 2. *Hemarthria fasciculata* (Lam.) Kunth. Enlarged and slightly excavated rachis joint showing the stalk of the pedicellate spikelet united with its margin and the specialization of the outer empty glume of the sessile spikelet.
- Fig. 3. *Coelorachis cylindrica* (Mx.) Nash. Deeply excavated and enlarged rachis joint showing the outer empty glume partly opened out to show the sessile spikelet and the stalked spikelet with vestigial glumes, situated at one side in front.
- Fig. 4. *Tripsacum dactyloides* L. The highly evolved, enlarged and deeply excavated rachis joint showing the outer empty glume serving as a lid to the box and enclosing the spikelet with the grain.
- Fig. 5. *Euchlaena mexicana* Schrad. Highly evolved, indurated, and perfected rachis joint enclosing the spikelets and grain completely, the indurated outer empty glume forming a closely fitting lid which is held down by the incurved edges of the box.



EXPLANATION OF THE FIGURES OF PLATE III.

All the stamens are drawn to the same scale of magnification.

- Fig. 1. *Agastache scrophulariaefolia* (Willd.) Ktz. An ordinary type of stamen with the two anther-sacs parallel and close together.
- Fig. 2. *Teucrium occidentale* Gr., showing the anther-sacs somewhat divergent.
- Fig. 3. *Clinopodium vulgare* L., showing the anther-sacs separated by the broadening of the connective.
- Fig. 4. *Satureia hortensis* L. The anther-sacs are still farther apart.
- Fig. 5. *Monarda didyma* L., showing a very prominent development of the connective with the anther-sacs divaricate.
- Fig. 6. *Salvia lyrata* L., showing the connective greatly elongated, appearing like a cross-bar between the two anther-sacs, the one of which is becoming vestigial because of the evolution of zygomorphy.
- Fig. 7. *Salvia officinalis* L. A more extreme development of the connective between the two anther-sacs, the one of which is decidedly reduced.
- Fig. 8. *Salvia lanceifolia* Poir. The connective has evolved into a well developed lever-bar and the vestigial anther-sac has disappeared.
- Fig. 9. *Salvia farinacea* Benth. The connective is longer and the handle end is more perfectly developed.
- Fig. 10. *Salvia pitcheri* Torr. The connective is still longer and the apparatus works as an ingenious pollination device.
- Fig. 11. *Salvia splendens* Ker-Gawl. The stamen has an enormously long connective, fitting with the long corolla tube.
- Fig. 12. *Salvia patens* Cav. The connective is not only much longer than in any of the preceding but the brush end of the lever is very much longer than the handle end.

